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FEEDING ECOLOGY OF SANDHILL CRANES DURING SPRING MIGRATION IN NEBRASKA

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Abstract: We studied the food habits of midcontinent sandhill cranes (*Grus canadensis*) during spring 1978 and 1979 at their primary staging area along the Platte River and compared population food and foraging habitat requirements with availability. Crane diets varied among the 3 principal foraging habitats, but not between sexes, ages, or years. Cranes feeding in cornfields ate >99% corn (total dry wt); those feeding in native grasslands and alfalfa fields consumed 79–99% invertebrates. The composite diet of cranes was 97% corn and 3% invertebrates, including 2% earthworms, 0.5% snails, and 0.5% insects. Presumably, corn provided energy, whereas invertebrates from grasslands and alfalfa fields provided supplemental nutrients to compensate for protein and calcium deficiencies in corn. The mean density of waste corn decreased ($P < 0.05$) from 399 kg/ha in November, to 205 kg/ha in early March, to 128 kg/ha after departure of the cranes. Simulations of population energetics indicated that 450,000–550,000 cranes would consume 20–25% of the waste corn available in the Platte River Valley during spring. Corn availability is unlikely to affect crane use of staging areas unless cropping practices or fall tillage reduce the acreage of harvested cornfields by >50%. Management by burning, haying, and grazing is compatible with crane use of grasslands, and reduced-till farming could benefit cranes by increasing invertebrate populations.

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A growing awareness of the impact of water resource development on spring staging habitat of sandhill cranes in the Platte River Valley of Nebraska has stimulated private, state, and federal conservation efforts (Krapu et al. 1982). Depletion of flows in the river has increased development of native wet meadows for crop production and reduced the width of river channels. This has concentrated cranes in restricted reaches of the river and caused concern that food resources needed to meet energy and nutrient requirements of the population may become inadequate. In particular, the role of grasslands in the feeding ecology of cranes needs more study (Wheeler and Lewis 1972, Reinecke and Krapu 1979).

Our research was part of a larger investigation of sandhill crane staging ecology (U.S. Fish and Wildl. Serv. 1981) that provided necessary background information to assess the management implications of population food and energy requirements. The objectives of our study were to: (1) relate qualitative aspects of food use to foraging habitat, (2) calculate daily and seasonal population food requirements, and (3) estimate food availability for comparison with projected requirements.

We thank C. R. Frith and R. J. Wicht for assistance in contacting landowners and the landowners of the Platte River Valley for access to their properties. D. Janke and D. Jenson contributed to our corn sampling project. B. A. Hanson assisted with insect taxonomy and, along with D. G. Jorde, R. E. Atkins, and G. R. Lingle, collected crane specimens. Molluscs and earthworms were identified by F. M. Uhler and W. N. Beyer, respectively. D. H. Johnson and A. M. Frank supervised the statistical analyses, and T. J. Dwyer and C. E. Korschgen reviewed the manuscript.

STUDY AREA

General features of the Big Bend Region of the Platte River in southcentral Nebraska have been described (U.S. Fish and Wildl. Serv. 1981). More detailed accounts of vegetation, hydrology, and land use are available in Wil-

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liams (1978), Currier (1982), and Krapu et al. (1984).

Midcontinent sandhill cranes use 3 separate staging areas along the Platte River during spring migration (Krapu et al. 1982). More than 350,000 cranes use Staging Area I, which extends from Grand Island to Kearney. Staging Area II, with about 50,000 cranes, lies between Elm Creek and Overton. Staging Area III is located west of North Platte and has 100,000 cranes. We collected data primarily from staging areas I and II and secondarily from Staging Area III.

Krapu et al. (1984) summarized land use for all 3 sites. Potential foraging habitats in Staging Area I included 53% row crops (primarily corn), 7% alfalfa, and 23% native grassland. Comparable estimates for Staging Area II were 38% row crops, 19% alfalfa, and 20% native grassland. Staging Area III had 28% row crops, 11% alfalfa, and 40% grassland. Native grasslands or wet meadows are mixed-grass prairies maintained by a high water table.

METHODS

Food Use

Feeding cranes were collected during March and early April 1978 and 1979 from cornfields, alfalfa fields, and native grasslands, the 3 principal foraging habitats (Krapu et al. 1984). Although we observed ≥10 minutes of foraging behavior prior to each collection, some birds lacked usable food samples. At times we observed cranes feeding on grasslands for as long as 30 minutes.

Each specimen was examined at a field laboratory following collection. After removing all food items from the esophagus, we determined sex by gonadal examination, age by plumage development (Lewis 1979), and subspecies by subjective comparison with criteria in Johnson and Stewart (1973:table 4). Later, food samples were sorted, identified, dried for 48 hours at 55 C, and weighed to the nearest 0.01 g. Two foods, shoots of winter wheat and alfalfa, were submitted to Hazleton Laboratories, Madison, Wisconsin, for proximate analysis. In this report, we have expressed the importance of foods as frequency of occurrence and percentage of total dry weight. Differences in frequency of use of foods among habitats and between years were summarized as contingency tables and tested with *G*-statistics (Sokal and Rohlf 1981).

Corn Abundance

We estimated the abundance of waste corn in November 1978 after fields were harvested, in late February 1979 prior to arrival of the cranes, and in April 1979 after crane migration. Details of the methods were presented by Frederick et al. (1984). Thirty cornfields were chosen at random from 180 sections of land comprising staging areas I and II. Three clusters of 3 plots were located at random within each field, and 1 plot from each cluster was sampled during each time period. A small plot was nested in the corner of each large plot; ears of corn were collected from the larger plot and kernels from the smaller.

During the summer of 1979 we interviewed farmers to determine grain yield and winter grazing pressure on the study fields. The acreage in corn production on the 3 staging areas was measured from 1:24,000 aerial photographs with an electronic digitizer. We analyzed the data on corn abundance using a 2-way analysis of variance (ANOVA) with fixed effects (time periods), random effects (fields), and plots nested within fields. Nonparametric correlation statistics were used to test for associations between changes in corn supplies and use by livestock and cranes (G. L. Krapu, unpubl. data).

Corn Requirements

We developed a computer program to simulate the food requirements of staging cranes at selected levels of population size and weight gain. The program calculated daily and cumulative food and energy needs as the product of individual requirements and population size; each age, sex, and subspecies was considered separately. Energy requirements were converted to food (corn only) intake with the assumptions that 97% of the diet was corn (this study) and that corn provided 3.85 kcal apparent metabolizable energy/g (dry wt) (Natl. Res. Counc. 1977:table 18).

Individual Requirements.—We followed the "integrative" method of Kendeigh et al. (1977: eqs. 5.18, 5.31) in calculating energy requirements. The daily metabolism of individuals in each age, sex, and subspecies was the sum of energy required for existence, free-living activity, and weight gains.

Temperature data were recorded at Kearney, Nebraska (Natl. Oceanic and Atmos. Adm. 1979). To calculate metabolism at 0 C, we used

published crane body weights (U.S. Fish and Wildl. Serv. 1981). Weights of juvenile male and female lesser sandhills (*G. c. canadensis*) were constant at 3,313 and 2,807 g, respectively; juvenile males and females of the larger subspecies (*G. c. tabida* and *rowani* combined) were constant at 4,353 and 3,640 g, respectively. Adult weights increased significantly during the stay in Nebraska. Data for adult lesser sandhills can be summarized as: males = 3,051 + 25.0 g × date; females = 2,927 + 13.6 g × date, where date increases from 1 on 1 March to 46 on 15 April. Weights for adults of the larger subspecies were: males = 3,972 + 22.1 g × date; females = 3,728 + 13.1 g × date. Finally, we increased daily energy requirements by 10% to allow for the costs of free-living activity (cf. Kendeigh et al. 1977:178) and accounted for daily weight gains using a conversion factor of 9.38 kcal/g of gain (Kendeigh et al. 1977:152).

Simulated Populations.—Sandhill cranes began arriving along the Platte River in late February or early March, increased rapidly in numbers until about 20 March, reached a peak population of >500,000 in late March or early April, and departed abruptly in April unless delayed by unfavorable weather (U.S. Fish and Wildl. Serv. 1981). We simulated daily crane numbers over a 46-day period from 1 March to 15 April for selected peak populations. First, crane numbers increased from 1 to 31 March according to the logistic equation:

$$\text{daily pop} = \text{peak pop}/(1 + e^{-0.35[\text{date}-15.5]}),$$

where peak population is specified and date ranges from 1 to 31. Then, crane numbers decreased from 1 to 15 April according to the reverse logistic equation:

$$\text{daily pop} = \text{peak pop} - \text{peak pop}/(1 + e^{-0.75[\text{date}-7.5]}),$$

where date ranges from 1 to 15. The percentages of the daily population allocated to staging areas I, II, and III were 69, 13, and 18%, respectively (U.S. Fish and Wildl. Serv. 1981:table 2). The proportion of larger crane subspecies increases from west to east (Krapu et al. 1982), and based on specimens collected in this study, we estimated that 50 and 95% of the cranes on staging areas I and II, respectively, were lesser sandhills. We assumed that all birds on Staging Area III were lessers. Sex and age ratios were 50 males:50 females and 88.4 adults:11.6 immatures (cf. Johnson and Stewart 1973, Buller 1979, Tacha and Vohs 1984). The sex, age, and taxonomic structure of the population was calculated as the product of the daily population and appropriate proportions.

RESULTS

Food Use

Sixty-nine esophageal food samples were available for analysis, including 34 from 1978; 35 from 1979; and 27, 23, and 19 from native grasslands, alfalfa fields, and cornfields, respectively (Table 1). Although most birds collected on native grasslands (89%, $N = 27$) and alfalfa fields (74%, $N = 23$) contained corn, we deleted corn from the analysis because it was unavailable in these habitats and occurred in the samples as a layer beneath other foods associated with the collection sites.

Use of plant and animal foods varied substantially among habitats (Table 1). The frequency of occurrence of plant foods in esophageal samples from cranes feeding in native grasslands was lower than in alfalfa fields (*G*-statistic, $P < 0.01$) and lower in alfalfa than in cornfields ($P < 0.01$). All birds from cornfields ate corn, and the dry matter intake was nearly 100%. Only 3 birds from native grasslands ate plant foods, and 2 of these contained tubers of an unknown grass or sedge. Use of plant foods was intermediate on alfalfa fields; 12 of 13 birds that ate plant foods contained alfalfa sprouts, which comprised 10–20% of the food intake. Sprouts of alfalfa and winter wheat submitted for proximate analysis contained 33.5% and 28.2% protein (dry wt), respectively.

The frequency of animal foods in the diet was higher for native grasslands than for alfalfa fields ($P < 0.01$) but did not differ between alfalfa and cornfields ($P > 0.5$). Although the frequency of invertebrates in food habit samples from alfalfa and cornfields was similar, invertebrates provided 79–99% of the total intake for native grasslands and alfalfa fields, but only a trace for cornfields.

Individual invertebrate taxa also varied in importance among habitats. Earthworms occurred with equal frequency in esophagi from native grasslands and alfalfa fields ($P > 0.5$) but rarely in those from cornfields ($P < 0.05$). Worms were the most important food from al-

Table 1. Foods from the esophagi of sandhill cranes collected in Nebraska during spring, 1978–79.

Food	Frequency of occurrence						% of total dry wt					
	Native grasslands		Alfalfa fields		Cornfields		Native grasslands		Alfalfa fields		Cornfields	
	1978 (*N* = 15)	1979 (*N* = 12)	1978 (*N* = 9)	1979 (*N* = 14)	1978 (*N* = 10)	1979 (*N* = 9)	1978 (*N* = 15)	1979 (*N* = 12)	1978 (*N* = 9)	1979 (*N* = 14)	1978 (*N* = 10)	1979 (*N* = 9)
Plant	2	1	4	9	10	9	1	2	10	21	100	100
Corn grain					10	9					100	100
Alfalfa shoots			3	9					9	19		
Grass leaves		1	1	1				2	1	2		
Miscellaneous	2						1					
Animal	15	11	5	8	4	6	99	98	90	79	tr[a]	tr
Gastropoda	6	10	2		1	1	23	26	7		tr	tr
Oligochaeta	6	8	4	7	1		39	56	76	75	tr	
Insecta	11	4	2	2	4	6	37	16	7	4	tr	tr
Orthoptera	4	1					21	2				
Coleoptera	8	3	1	2	2	5	14	14	1	4	tr	tr
Carabidae	5	2	1	2	1	5	2	12	1	4	tr	tr
Others	3	1			2		12	2			tr	
Lepidoptera	3		2		2	2	2		6		tr	tr
Others[b]	5		1				tr		tr			

[a] tr = <0.5%.
[b] Primarily isopods and arachnids.

falfa fields, contributing 75% of the dry weight. We could not identify the species of earthworm in the food samples because most were immature (aclitellate) and damaged by the cranes. Mature worms collected from several foraging sites were *Aporrectodea trapezoides*, a widely distributed species introduced to North America from the Palearctic (Edwards and Lofty 1977).

Insects provided 16–37% of the food of cranes from native grasslands and were consumed more frequently in this habitat than in alfalfa fields ($P < 0.05$). Although ground beetles (Carabidae) and corn borers (Pyralidae) occurred regularly in esophagi of cranes from cornfields, the total intake was minimal. Cranes foraging in alfalfa fields ate only a few ground beetles and cutworms (Noctuidae), whereas food habit samples from native grasslands contained crickets (Gryllidae), grasshoppers (Acrididae), ground beetles, rove beetles (Staphylinidae), scarab beetles (Scarabaeidae), click beetles (Elateridae), and cutworms.

Nearly 25% of the diet of cranes from native grasslands was snails. Food habit samples from native grasslands contained snails more often than samples from either alfalfa or cornfields ($P < 0.01$). All 7 cranes that ingested the most snails were collected on native grasslands, including 5 birds that ate from 17 to 63 empty snail shells. Seventeen of the 20 cranes ingesting snails had eaten a terrestrial species, *Succinea* spp., which we observed regularly in wet grasslands and occasionally in alfalfa fields.

We did not collect enough immature cranes (7 of 69 food samples) to compare quantitatively food use between ages. However, juveniles ate the same foods as adults, including corn, alfalfa sprouts, isopods, adult and larval insects, worms, and snails. We also did not detect any differences in the occurrence of plant and animal foods between males and females or between years ($P > 0.1$).

Cranes collected from the 3 habitats differed not only in the type of food ingested but also in the quantity of food accumulated ($P < 0.001$). Average food sample dry weights (g ± SE) for native grasslands, alfalfa fields, and cornfields were 0.61 ± 0.17, 0.70 ± 0.08, and 22.8 ± 2.7, respectively. A Student-Newman-Keuls multiple comparison test indicated that sample weights for native grasslands and alfalfa were similar ($P > 0.5$), but those from cornfields were heavier ($P < 0.01$).

To compare the amount of corn used by cranes to its abundance on the staging areas, we needed an average or composite daily diet. Simply adding the quantities of food from each habitat would have been biased because sample sizes (this study) and daily use (Krapu et al. 1984) varied among habitats. To compute the proportion of each food in the composite diet,

Table 2. Changes in the density of waste corn (arithmetic means in kg/ha) on staging areas I and II in the Platte River Valley, Nebraska, 1978–79.

Type of corn sampled	Time of sample collection[a]				
	After corn harvest (N = 30 fields)	P[b]	Before crane arrival (N = 29 fields)	P	After crane departure (N = 25 fields)
Kernel	100	<0.05	85	<0.05	38
Ear	299	<0.05	120	<0.05	90
Total	399	<0.05	205	<0.05	128

[a] After corn harvest = early Nov 1978, before crane arrival = early Mar 1979, after crane departure = early Apr 1979.
[b] P = significance level from Duncan's test for differences between means in adjacent columns.

we: (1) weighted the quantity of each food from each habitat by the sample size (from Table 1) and proportion of daily use (Krapu et al. 1984: table 2) for that habitat, (2) summed this quantity over habitats, and (3) divided by the sum over all such foods:

$$P_1 = \sum_{i=1}^{m} Q_{1,i}/K_i \times W_i/$$

$$\sum_{j=1}^{n} \sum_{i=1}^{m} Q_{j,i}/K_i \times W_i,$$

where

P_1 = the proportion of food 1 in the composite diet,
$Q_{1,i}$ = the quantity of food 1 in samples from habitat i,
K_i = the sample size for habitat i,
W_i = a weighting factor for daily use in habitat i,
$Q_{j,i}$ = the quantity of food j in samples from habitat i, and
m and n = the number of habitats and foods, respectively.

Calculated in this way, plant and animal foods provided 97 and 3% of the diet, respectively, including 97% corn, 2% earthworms, 0.5% insects, and 0.5% snails.

Corn Abundance

Planimetry of August 1979 aerial photography indicated that 27,093; 9,087; and 4,914 ha were in corn production on staging areas I, II, and III, respectively. During November 1978, we sampled waste corn on 31 fields in staging areas I and II. One field suffered severe hail damage and was deleted from the analysis. The number of samples obtained following crane migration decreased further as a result of spring tillage.

The mean abundance of waste corn sampled in early November (30 fields) was 399 kg/ha; 75% of this waste occurred as ears (Table 2). Harvest on our sampling sites (29 fields) averaged 6,235 kg/ha (range = 1,481–11,111). Waste corn as a percentage of harvest averaged 8% (range = 2–33%).

For the ANOVA of changes in corn abundance over time, we transformed all variates to $\ln(\bar{x} + 1)$, because field means were correlated with variances (e.g., $r = 0.79$, $P < 0.001$ in fall), and we only analyzed fields with complete data (25 fields). The 2-way ANOVA rejected the hypothesis of equal corn density over time ($P < 0.001$), and Duncan's test confirmed that there were changes in kernel, ear, and total corn density between time periods ($P < 0.05$, Table 2). By early March, corn density had decreased to 205 kg/ha (29 fields), with larger losses of ear corn (60%) than kernel corn (15%) during winter. Fields sampled after migration in April averaged 128 kg/ha (25 fields), with larger losses of kernel corn (55%) than ear corn (25%) during spring.

The ANOVA also detected variation among fields ($P < 0.001$) and a field × period interaction ($P < 0.001$). We calculated Spearman correlation coefficients to test for associations between winter corn losses and cattle use, and spring losses and crane use. None were significant ($r = 0.15-0.29$, $P > 0.1$), but all were positive, an unlikely event ($P < 0.02$) if no relationship existed.

Corn Requirements

We simulated energy and food requirements for crane populations of 450,000; 500,000; and 550,000 and compared requirements with and without the productive energy needed for weight gains by adults. At the individual level juvenile body weights were held constant, and food requirements varied only with subspecies, sex, and temperature. Within days, young males and females of the larger subspecies needed 15% more corn than lesser sandhills (106 and 97 vs. 91 and 84 g, respectively); male requirements exceeded those of females by 9–10%. Maximum simulated food requirements for immatures occurred on 5 March at an average temperature of −4.4 C and were 16% greater than the minima on 8 April at 13.6 C; i.e., 93 vs. 80 g for male lesser sandhills.

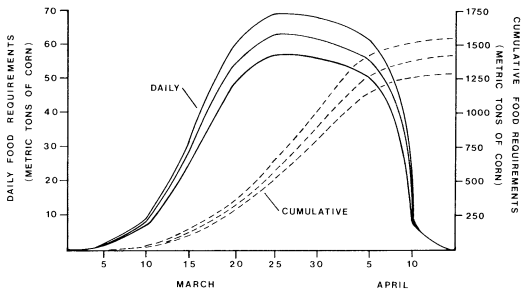

Fig. 1. Simulated daily and cumulative food (corn) requirements during the spring staging period for projected populations of 450,000; 500,000; and 550,000 cranes.

Adult requirements varied within days as a function of subspecific and sex-specific weights and weight gains. For example, male lesser sandhills needed 25% more corn than females on day 1 but also gained weight more rapidly; on day 46 they needed 30% more food. Day-to-day changes in adult requirements were more complex than for juveniles. Both ambient temperatures and body weights increased during the staging period but had a compensatory effect on metabolism. Maximum adult food needs occurred on 18 March and were 10% greater than the minima on 13 April; i.e., 159 vs. 144 g for male lesser sandhills. When we omitted energy used for fat deposition, the simulated corn requirements of respective adult male and female lesser sandhills decreased 69 and 39% and of the larger subspecies 53 and 33%.

At the population level food requirements were determined primarily by population size (Fig. 1). Maximum daily energy requirements for staging populations of 450,000; 500,000; and 550,000 cranes were 235, 261, and 287 million kcal, respectively; maximum daily food requirements were 58, 65, and 72 metric tons of corn, respectively. Maximum requirements occurred 2 days after peak populations because of low temperatures on 2 April. Cumulative food needs for the 3 populations were 1,323; 1,471; and 1,617 metric tons of corn during the staging period. For a peak population of 500,000 cranes, corn use on staging areas I, II, and III was 1,023; 188; and 259 metric tons, respectively. Productive energy needed for fat deposition accounted for 29–30% of the maximum daily and cumulative food requirement.

DISCUSSION

Invertebrates

Our data indicate that sandhill cranes are omnivorous and opportunistic (e.g., Guthery 1976, Mullins and Bizeau 1978) and feed extensively during spring in Nebraska cornfields (Lewis 1974). However, we also gained new insight into the variation in diet among habitats. Foods from native grasslands and alfalfa fields included 79–99% invertebrates and were good sources of protein and calcium. Conversely, cornfields provided <1% invertebrates, but the corn was rich in carbohydrates and energy. Ground beetles and larval corn borers probably were eaten whenever encountered in cornfields but apparently were not abundant enough to balance the diet. Although native grasslands and alfalfa fields both provided invertebrates, the food resources of native grasslands were more diverse. Cranes collected from native grasslands ate worms, several taxa of insects, and snails, whereas birds from alfalfa fields ate only worms and alfalfa shoots. It seems likely that cranes graze on alfalfa to offset the lack of invertebrate diversity in alfalfa fields because emerging alfalfa shoots have a protein content (33.5%) comparable to arrowgrass (*Triglochin palustris*) (30.1%), which supports rapid growth in goslings of the cackling goose (*Branta canadensis minima*) (Sedinger and Raveling 1984). Thus, regular changes in foraging habitat during spring are associated with important changes in food resources and suggest that foraging behavior is influenced by nutrient requirements.

To analyze nutritional constraints on foraging behavior, we must consider nutrient balances during the staging period; i.e., do cranes gain, lose, or maintain an equilibrium with respect to body fat, protein, and calcium? Data collected concurrently with our study demonstrated that cranes store substantial fat during the staging period (Krapu et al. 1985) but that body protein (Krapu et al. 1985) and calcium (K. J. Reinecke and G. L. Krapu, unpubl. data) are unchanged. Dietary protein and calcium intake, therefore, should reflect maintenance requirements, whereas energy intake should be elevated to support fat deposition.

That invertebrates provide cranes with required nutrients follows from an analysis of foraging efficiency, wherein both time and energy measure the value of foods in the diet. For example, we know that cranes spend similar amounts of time foraging in cornfields and grasslands during spring (Krapu et al. 1984) but obtain less food from grasslands (this study). Accordingly, cranes allocate as much time to obtaining 3% of their diet in the form of invertebrates as to the 97% that is corn. The value

of invertebrates in the diet is most likely an increase in protein and calcium intake; the percentage of protein in field corn is marginal and that of calcium very low (Natl. Res. Counc. 1977:table 18) compared to the requirements of chickens (Natl. Res. Counc. 1977:tables 2, 3).

Further analysis suggests that the supplemental calcium from invertebrates is important quantitatively and the protein qualitatively. For example, if an adult male lesser sandhill eats 143 g of corn on day 1 of the staging period, and the composite diet is 97% corn, then he also eats 4.4 g of invertebrates. This would include 0.7 g of snails (mostly shells) containing approximately 40% calcium (Natl. Res. Counc. 1977:table 21), or about 0.3 g of calcium. A crane would have to consume nearly 1,500 g of corn to obtain an equivalent amount, and this would require an unrealistic foraging effort (normally 143 g of corn in 2–3 hours foraging). The fact that some cranes excavate and ingest lime nodules (K. J. Reinecke and G. L. Krapu, unpubl. data) also supports the argument that corn is deficient in calcium.

Cranes would gain about 2 g of protein by including insects and worms in their diet. However, 20 g of corn at 10% protein (Natl. Res. Counc. 1977:table 18) would provide the same benefit with a smaller investment of foraging time. That cranes choose to search for invertebrates suggests that corn satisfies quantitative but not qualitative (amino acid) protein requirements.

Daily foraging effort in birds generally is determined by energy requirements (Mayer et al. 1979); exceptions involve females seeking nutrients for egg production (Beasom and Pattee 1978) or migrants storing reserves prior to nesting (McLandress and Raveling 1981). Our study has documented nutrient limitations in cranes that were depositing fat but not protein.

Corn

Frederick et al. (1984) analyzed corn sampling data from 3 study areas, including Nebraska, and concluded that the density of waste corn in the Platte Valley was not different from that in the High Plains of western Texas or the Missouri River Valley of Iowa. Although total and ear corn decreased 49 and 92%, respectively, during winter in Nebraska, we found only a weak correlation between grazing intensity and changes in corn abundance. In Texas, winter grazing removed 84% of all corn and 97% of the ear corn (Baldassarre et al. 1983). During spring, kernels accounted for 61% of corn losses, and changes in kernel density were positively but not significantly related to crane use. We concluded that ear and kernel corn losses during winter and spring were probably the result of grazing and crane use but that additional sampling would be needed to study these changes.

To illustrate the relationships between population food use and foraging habitat requirements, we synthesized data on: (1) mean density of corn/ha, (2) ha in corn production, (3) ha of corn modified by fall tillage, (4) population food requirements, and (5) the lowest density of corn that attracts foraging cranes (Table 3). Estimates of (1), (2), and (4) were presented in Results, and 2 sources of data were available for (3), the impact of tillage on corn abundance. During studies of crane and mallard (*Anas platyrhynchos*) habitat selection, Krapu et al. (1984) and Jorde (1981) estimated that 39 and 9% of the cornfields in portions of staging areas I and II, respectively, were tilled during fall. Regarding (5), we found little evidence for the existence of a minimum corn density that limited foraging by cranes. Some samples taken following departure of the birds contained no corn at all, whereas others had ≤332 kg/ha. If cranes consistently switched from low to high corn density sites, variation among fields should have decreased from harvesting through the arrival and departure of the cranes. However, the coefficient of variation increased over this period (CV = 0.6, 0.7, and 1.0, respectively).

Table 3 compares corn requirements and availability, expressed as ha of habitat providing 205 kg corn/ha, by staging area and population size. We considered 3 rates of food exploitation and 4 levels of fall tillage. Because current estimates indicate that crane populations and fall tillage are close to 500,000 and 25%, respectively, corn supplies undoubtedly exceed requirements at present, assuming cranes can recover 50% of the waste grain. This conclusion also is supported by other evidence. A peak population of 500,000 cranes needs about 1,471 metric tons of corn; this represents only 23% of the 6,519 metric tons present in spring and is small compared to the 4,070 metric tons remaining after migration. We also know that cranes deposit substantial quantities of fat during the staging period (Krapu et al. 1985), forage at a moderate rate (Krapu et al. 1984), and travel ≤3–5 km to daily feeding sites (U.S. Fish and Wildl. Serv. 1981). Corn will be in short

Table 3. Hectares of harvested cornfields necessary to support the sandhill crane population in the Platte River Valley, Nebraska, under selected conditions.

Staging area	Hypothetical crane population (thousands)	Cumulative food requirement (10^3 kg corn)	Area of cornfields required (10^3 ha) assuming cranes remove[a]			Area of cornfields available (10^3 ha) assuming fall tillage is[b]			
			100%	75%	50%	75%	50%	25%	0%
I	310	887	4.3	5.8	8.7				
	345	986	4.8	6.4	9.6	8.8	14.9	21.0	27.1
	379	1,084	5.3	7.1	10.6				
II	59	163	0.8	1.1	1.6				
	65	181	0.9	1.2	1.8	3.0	5.0	7.0	9.1
	72	199	1.0	1.3	1.9				
III	81	225	1.1	1.5	2.2				
	90	250	1.2	1.6	2.4	1.6	2.7	3.8	4.9
	99	275	1.3	1.8	2.7				
Combined	450	1,275	6.2	8.3	12.4				
	500	1,417	6.9	9.2	13.8	13.4	22.6	31.8	41.1
	550	1,558	7.6	10.1	15.2				

[a] Assumes that waste corn abundance in spring is 205 kg dry wt/ha (Table 2).
[b] Assumes that tillage reduces corn availability by approximately 90% (Baldassarre et al. 1983).

supply only if fall tillage or changes in cropping practices affect 50–75% of the acres in production. Continued crowding of cranes into Staging Area I could cause a shortage at a tillage rate of 50%.

MANAGEMENT IMPLICATIONS

An agricultural economy based on corn and livestock is beneficial for sandhill cranes staging in the Platte River Valley. Cattle that graze on grasslands in summer are pastured on harvested cornfields in winter. In our study 26 of 30 corn sampling sites were grazed after harvest. As much as 6,000 metric tons of corn may be recovered by farmers in this way, and the remainder, mostly kernels, provides adequate energy for the cranes. If fall tillage or changes in cropping practices reduce the acreage of harvested cornfields by 50–75%, then crane body weights, foraging effort, and distribution should be re-evaluated.

At present, grassland invertebrates are the food resource in short supply. Although alfalfa fields can support substantial earthworm populations (Edwards and Lofty 1977) and were a valuable source of food for cranes, natural grasslands provided a greater diversity of invertebrates, including worms and several taxa of insects and snails. Primary management efforts should be directed toward maintaining or increasing invertebrate populations.

Several options exist for management of grassland and cropland. Burning, grazing, and haying can each provide the short stands of vegetation preferred by cranes. Burning temporarily reduces above-ground community structure and diversity (Morris 1971) but seems to have a favorable effect on soil fauna (Lussenhop 1976). Cranes responded immediately to an experimental burn in a stand of big bluestem (*Andropogon gerardi*), switchgrass panicum (*Panicum virgatum*), and yellow Indiangrass (*Sorghastrum nutans*) during April 1978, and 2 birds collected at the site had eaten earthworms. Spring burning may promote worm activity by increasing solar radiation and soil temperatures (Gerard 1967). Burning also retards succession and maintains high organic matter production in grasslands; earthworm populations vary with the quantity and quality of soil organic matter (Edwards and Lofty 1977). Another option is controlled grazing. Returning organic matter to the soil as manure benefits worms (Edwards and Lofty 1977), and the cycling of organic matter is increased when birds break up dung searching for invertebrates and grain (Anderson and Merritt 1977).

Reduced-till farming practices might be used to increase invertebrate populations on cropland, especially where managed to attract cranes for public viewing. Edwards and Lofty (1980, 1982) showed that worm populations increase when annual tillage ceases. However, continuous cropping gradually depletes soil organic matter, which must be periodically restored via rotation. Burning reduced-till cropland might be a way of increasing availability of both grain (Baldassarre and Bolen 1984) and invertebrates.

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